A MULTIVARIATE MORPHOMETRIC ANALYSIS OF THE *SOLIDAGO CHILENSIS* GROUP IN SOUTH AMERICA AND RELATED TAXA IN NORTH AMERICA (ASTERACEAE, ASTEREAE)[1]

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ABSTRACT

A multivariate morphometric study of *Solidago* L. in South America was undertaken to assess the numbers and ranks of taxa that could be usefully recognized. The results of stepwise discriminant, classificatory, and canonical analyses on a matrix of 50 traits of 160 specimens indicated the distinctiveness of the *S. chilensis* group of taxa from three morphologically similar North American species of the large *Solidago* subsect. *Triplinerviae* (Torr. & A. Gray) G. L. Nesom: *S. juliae* G. L. Nesom, *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott. Within the South American complex two species with predominantly allopatric distributions were statistically supported: *S. chilensis* Meyen and *S. microglossa* DC. were distinguished a priori on stem hair length. The cytogeography of the two species was investigated and all samples were diploid, $2n = 18$; *S. chilensis* (20 individuals from Argentina and one from Chile) and *S. microglossa* (six individuals from Argentina). Also, two other species of *Solidago* in South America that are not members of subsection *Triplinerivae* were found to have been misidentified as members of the *S. chilensis* complex; European *S. virgaurea* L. is a member of *Solidago* subsect. *Solidago* and native *S. argentinensis* Lopez Laphitz & Semple is a member of *Solidago* subsect. *Junceae* (Rydb.) G. L. Nesom. The name *S. chilensis* is neotypified.

Key words: Asteraceae, biogeography, cytogeography, multivariate morphometrics, *Solidago*.

The goldenrod genus *Solidago* L. (Asteraceae, Astereae) includes some 120 species primarily native to North America with a few species native to South America and a half dozen or more native to Eurasia (Semple, 2015). Semple and Cook (2006) recognized 77 species native to Canada and the United States, but more recent work indicates that as many as 103 species occur in the two countries (see Semple, 2015). The genus is divided into 13 subgeneric groupings with the taxonomically challenging *Solidago* subsect. *Triplinerviae* (Torr. & A. Gray) Nesom being the largest, with some 16 species. Members of subsection *Triplinerviae* are distinguished by (1) the absence of basal rosettes, (2) by having lower stem leaves that nearly always wither by flowering and that are not as large as lower mid-stem leaves, and (3) by having lower and mid-stem and sometimes upper stem leaves that are 3-nerved due to two lateral nerves being prominent (Semple & Cook, 2006). Heads are usually arranged in secund pyramidal inflorescence arrays. Pappus bristles are usually in two series that are sometimes similar, with the longer inner series usually weakly if at all clavate or rarely moderately so (Hood & Semple, 2003).

Multivariate studies on three sets of species in *Solidago* subsect. *Triplinerviae* have been investigated recently. *Solidago brendiae* Semple, *S. canadensis* L., *S. elongata* Nutt., *S. fallax* (Fern.) Semple, and *S. lepida* DC. were examined in one study (Semple et al., 2013), and *S. altiplanities* C. E. S. & R. John Taylor, *S. altissima* L., *S. canadensis*, and *S. juliae* G. L. Nesom were examined in a second study (Semple et al., 2015). Lopez Laphitz (2009) investigated the South American goldenrods in the *S. chilensis*/*S. microglossa* group and compared them to the morphologically similar North American species *S. juliae*, *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott of the informal Tortifolia group of *Solidago* subsect. *Triplinerviae* (Nesom, 1994; Semple, 2015). The results of this latter multivariate study are presented here.

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Lopez Laphitz et al. (2011) presented evidence that some South American collections identified as *Solidago chilensis* in the broad sense were in fact members of *Solidago* subsect. *Junceae* (Rydb.) G. L. Nesom and belonged in a new species, *S. argentinensis* Lopez Laphitz & Semple, closely related to the western North American *S. missouriensis* Nutt. Lopez Laphitz (2009) also noted that an Argentine specimen identified as *S. patagonica* Phil. was an escaped cultivar of *S. virgaurea*, a species native to Europe; *Cabrera 5015* (LP) was annotated as *S. virgaurea* by J. C. Semple in 2009. Sancho and Viera Barreto (2014) included this observation in their treatment of *Solidago* in Flora Argentina.

The number of ranks of taxa recognized in the literature on *Solidago* in South America has varied over time. Some 29 basionyms based on South American collections have been proposed, the majority for plants from Chile and Brazil (Hooker & Jackson, 1895, and supplements). Cabrera (1970) proposed the combination *S. chilensis* var. *megapotamica* (DC.) Cabrera and listed *S. microglossa* DC. as a synonym. Cabrera (1971) recognized two species, *S. chilensis* with densely headed inflorescences and *S. patagonica* sensu Cabrera with a sparsely headed inflorescence, in his treatment of *Solidago* in the Flora of Patagonia, basing the latter on *Cabrera 5015* (LP) by using head density to separate the two species. Cabrera (1974) recognized the one species *S. chilensis* with two varieties, glabrous variety *chilensis* and pubescent variety *megapotamica*, in his treatment of *Solidago* in the Flora Ilustrada Entre Rios (Argentina). Following Cabrera (1974), Sancho and Espinar (2003) recognized the same two varieties of *S. chilensis* in Flora Fanerogámica Argentina, again separating glabrous variety *chilenis* from pubescent variety *megapotamica*. Most recently, Sancho and Viera Barreto (2014) recognized three species of *Solidago* in Flora Argentina: *S. argentinensis*, *S. chilenis* (with variety *chilensis* and variety *megapotamica*), and *S. virgaurea* (based on *Cabrera 5015*, LP).

Kress et al. (2005) stated that genetic barriers among species of *Solidago* are poorly developed, and, consequently, a phylogeny of the genus had been difficult to obtain. While Brouillet et al. (2009) were successful in resolving the phylogeny of the tribe Astereae using ITS, Schilling et al. (2008) reported on a lack of resolution in the phylogeny of *Solidago* based on sequence data due to very low levels of variation in ITS and ETS. They concluded that the restriction fragment length polymorphisms based phylogenies in Zhang (1996; one phylogeny reproduced in Semple et al., 1999) were the only informative molecular phylogenies for the genus. No South American species of *Solidago* were included in Zhang (1996). Until more phylogenetically informative sequences are discovered in *Solidago*, alternative nonmolecular methods must be utilized to assess species limits within the genus.

Taxonomic treatments on *Solidago* in South America were based mainly on floristic descriptions only, and no multivariate study has ever been conducted on *S. chilensis* s.l. In order to determine the number of taxa in the complex and to assess the distinctiveness of members of the South American group from North American relatives, a multivariate morphometric analysis was undertaken. Because *S. chilensis* s.l. had been included in *Solidago* subsect. *Triplinerviae* at the time this study was initiated in 2007, three morphologically similar North American species of this subsection were included in the analysis for comparison.

The names of taxa used in this report are those accepted at the conclusion of this study.

METHODS

SPECIMENS

A total of 552 herbarium specimens, including those in WAT and specimens borrowed from other herbaria in the United States, Argentina, and Madeira (AAH, BRIT, GH, LL, LP, MADM, MO, and TEX), were examined. Of these, 350 herbarium specimens of *Solidago chilensis* s.l. were examined. Additionally, 52 specimens collected during a field trip through Argentina and Chile during May 2008 were included in the investigation. From all of these specimens, 118 specimens of *S. chilensis* and *S. microglossa* were selected for inclusion in the multivariate analyses based on the stage of floral development and completeness of the collection, i.e., those including at least mid- and upper stem and leaves and heads in anthesis. Using traits included in other analyses on the genus, descriptions of the taxa found in the literature (Semple & Cook, 2006), and personal observations, a list of the potentially useful and distinguishing traits was created (Table 1). Fifty morphological and floral traits were scored on these specimens. A 160-sample matrix of South American and related North American specimens was ultimately divided into five a priori groups; the numbers of individuals in each species-level a priori group were *S. tortifolia* (15), *S. juliae* (11), *S. leavenworthii* (15), *S. chilensis* (88), and *S. microglossa* (31). Location information on all South American collections examined was included in Lopez Laphitz (2009). Location information on North American collections is available on request from J. C. Semple.

Table 1. Traits characterized and measured for *Solidago chilensis* Meyen, *S. microglossa* DC., and related taxa from North America (*S. leavenworthii* Torr. & A. Gray, *S. juliae* G. L. Nesom, *S. tortifolia* Elliott). Traits with an asterisk (*) were not included in discriminant analyses because they correlated strongly (correlation coefficient of $|r| > 0.7$) with another trait or there were not enough measurements to be considered representative. Traits marked with the # symbol were also excluded as they were used to identify a priori groups in some analyses. Character codes are followed by their description.

Character code	Description
STEMHT*	stem height (cm)
ISTPUBD	stem hairs—number of hairs counted on 1 mm on inflorescence stem
USTPUBD*	stem hairs—number of hairs counted on 1 mm on upper vegetative stem
MSTPUBD*	stem hairs—number of hairs counted on 1 mm on midstem
BSTPUBD	stem hairs—number of hairs counted on 1 mm on basal stem
ISTHLN	hair length (mm) measured on inflorescence stem
USTHLN*	hair length (mm) measured on upper vegetative stem
MSTHLN*	hair length (mm) measured at midstem
BSTHLN*	hair length (mm) measured at basal stem
BLLENG*	basal leaf length (cm) measured from leaf base to apex
BLWID*	basal leaf width (cm) measured at widest point of blade
BLWTOE*	basal leaf (cm) measured from widest point to blade apex
BLSERAT*	basal leaf dentation counted as # of serrations on 1/2 of leaf margin
MLLENG	midstem leaf length (mm) as measured from leaf base to apex
MLWID	midstem leaf width (cm) as measured from widest point to blade apex
MLWTOE*	midstem leaf (mm) as measured from widest point to blade apex
MLSERAT#	midstem leaf dentation—number of serrations on 1/2 of margin
ULLENG	upper stem leaf length (mm) measured from leaf base to tip
ULWID	upper stem leaf width (mm) measured at widest point
ULWTOE*	upper stem leaf measured from widest point to tip (mm)
ULSERAT#	upper stem leaf dentation—number of serrations on 1/2 of leaf margin
ILLENG	inflorescence leaf length (mm) measured from leaf base to tip
ILWID	inflorescence leaf width (mm) measured at widest point
ILWTOE*	inflorescence leaf measured from widest point to tip (mm)
ILSERAT#	inflorescence leaf dentation—number of serrations on 1/2 of leaf margin
CAPBRANG	angle formed between main stem and branch measured from inflorescence
CAPW	width of inflorescence measured at widest point (cm)
CAPL	length of inflorescence measured from base to tip (cm)
LONGBR	length of longest branch in inflorescence (cm)
INVOLHT*	height of involucre (cm)
OPHYLL	outer phyllary length (mm) measured from phyllary base to tip
OPHYLW	outer phyllary width (mm) measured at widest point
OPHYLWTOE*	outer phyllary measured from widest point to tip (mm)
OPHYLV	outer phyllary number of veins
IPHYLL	inner phyllary length (mm) measured from phyllary base to tip
IPHYLW	inner phyllary width (mm) measured at widest point
IPHYLWTOE*	inner phyllary measured from widest point to tip (mm)
IPHYLV	inner phyllary—number of veins
RFLOR	number of ray florets per head
RSTRAPL	ray lamina length (mm) measured from top of corolla tube to tip of lamina
RSTRAPWD*	ray lamina width (mm) measured at widest point
RACHL*	ray floret cypsela length (mm) at anthesis stage
RPAPL	ray floret pappus length (mm)
DFLOR	number of disk florets per head
DCORL	disk corolla tube length (mm) measured from base to tip of corolla tube
DACHL	disk floret cypsela length (mm) at anthesis stage
DCORLIMB*	disk floret corolla limb length (mm)
DLOBL	disk corolla lobe length (mm)
DPAPL	disk pappus length (mm)
BRANCHD*#	distance between the first two branches at base of inflorescence

Assignment of the 160 specimens to the five a priori groups was based on morphological characters used in the literature to separate the taxa (Semple & Cook, 2006), on characters identified by us, and on provenance. Specimens were assigned a priori to *Solidago juliae* based mainly on geographical distribution, specifically presence on the Edwards Plateau and in Trans-Pecos, Texas, and adjacent Mexico; stems densely hairy with generally short hairs 0.5 ± 0.1 mm long and leaves grayish green due to high hair density. Following Semple and Cook (2006), the number of serrations in mid-stem leaves was used to identify *S. leavenworthii*; these plants came from the outer coastal plain of Georgia and Florida. Specimens placed a priori in *S. tortifolia* came from the outer coastal plain from South Carolina to Louisiana and had smaller involucres than *S. leavenworthii* following Semple and Cook (2006). Illustrations and the ranges of these three North American species are shown in Semple (2015, continuously updated).

MULTIVARIATE ANALYSES

Univariate and multivariate statistical analyses were performed using SYSTAT 10 for Windows (SPSS Inc., 2000, Chicago, Illinois, U.S.A.). Discriminant analysis is a well-known tool in taxonomy. It has been used successfully in *Solidago* (e.g., Heard & Semple, 1988; Semple et al., 1990; Cook et al., 2009; Semple et al., 2013, 2015) and in other Astereae (Owen et al., 2006). It was used in this study to assess the distinctiveness of members of the *S. chilensis* complex from the North American relatives. It allows testing of the usefulness of key traits in published floristic treatments (e.g., density of the paniculiform inflorescence; Cabrera, 1971). Also, it provides critical statistical information on the probabilities that an individual specimen belongs in each group included in the analysis. Correct placement a posteriori into the a priori group can occur but with a low probability. The number of such specimens with low probabilities of placement is an indication of the distinctiveness of pairs of taxa. The goal is to find traits that have low within-group variance but high between-group variance.

Discriminant analysis consists of a set of subanalyses. First, a pairwise Pearson correlation matrix was generated to determine which traits were highly correlated. When pairs of traits were correlated with $|r| > 0.7$, one trait of the pair was dropped from further analyses. This is done on the assumption that highly correlated traits may be under the control of a single gene with pleiotropic effects.

Then, using only the less correlated characters, stepwise discriminant analysis was used to select a subset of characters that maximize the Mahalanobis distances separating the a priori groups in N-dimensional hyperspace; these selected characters were then used to run a complete discriminant analysis. The number of characters that can be used is one less than the smallest sample size in any a priori group. Characters used are selected based on the F-statistic of removal, with larger F-values indicating greater importance in separating a priori group centroids in N-dimension hyperspace. Next, classificatory discriminant analyses (linear and jackknife) were performed on the data matrix using traits identified by the stepwise analysis and a discriminant function to assign individual specimens to groups a posteriori. Included in these analyses were tests for equality of group centroids (Wilks' lambda, Pillai's trace, and Hotelling-Lawley trace) for testing null hypotheses and the determination of Geisser assignment probabilities of a posteriori placement of each specimen into each a priori group. Finally, a canonical discriminant analysis was used as a dimension-reduction technique to facilitate visualization of the results of the multidimensional analyses.

Initially, a subset of 110 South American specimens was analyzed to assess character variation and test hypotheses on the number of taxa. Then, a discriminant analysis was performed on the full 160-sample matrix in order to assess differences between North American and South American members of *Solidago* subsect. *Triplinerivae* and as a way of assessing the level of difference between the two South American a priori groups compared to the three North American species-level a priori groups.

CYTOLOGY

Mitotic chromosome numbers were determined from root tip cells of plants grown from field-collected cypselae at the University of Waterloo Department of Biology greenhouse following Owen et al. (2006). Counts were made from cells of freshly squashed root tips. Vouchers of all collections have been deposited in WAT with duplicates in LP.

RESULTS

The means, standard deviations, and ranges of the 50 traits scored on 160 specimens of *Solidago chilensis*, *S. juliae*, *S. leavenworthii*, *S. microglossa*, and *S. tortifolia* were calculated and are presented in Table 2.

PRELIMINARY DISCRIMINANT ANALYSES

Three preliminary discriminant analyses were performed to test support for hypothesized taxa in South America using only the 116 specimens from South America; naturalized collections of *Solidago chilensis* from Madeira Island and the West Indies were not included. The distribution of South American specimens included in the analysis is shown in Figure 1; ranges are based on Lopez Laphitz (2009). Details for all analyses were presented in Lopez Laphitz (2009). First, in order to test the usefulness of a published floristic key (Cabrera, 1971), a two a priori group analysis was performed: *S.* "*patagonica*" with lax inflorescence and *S. chilensis* with dense inflorescence. Although the two groups differed significantly overall (i.e., the null hypothesis that the two groups were not different was rejected; alpha < 0.05), a posteriori assignment probabilities of individual specimens were often low and misclassifications were frequent. In a second discriminant analysis, hair density was used to define two varietal level a priori groups: *S. chilensis* s.l. with a high hair density (variety *megapotamica* sensu Cabrera) and *S. chilensis* with no hairs (glabrous; variety *chilensis* sensu Cabrera). Again, although the two groups differed significantly and the null hypothesis was rejected, a posteriori placement of many individuals had low probabilities of correct placement and many specimens were misclassified. Third, based on our observations, the *S. chilensis* complex was tentatively split into two putative species-level taxa based on the mid-stem hair length: *S. chilensis* with short hairs (mean of 0.2 ± 0.1 mm long) and *S. microglossa* with long hairs (mean of 0.9 ± 0.15 mm long). In the classificatory discriminant analysis, correct a posteriori assignments occurred for more than 90% of the individuals included in the analysis for both of the putative taxa. Following these results, two species-level groups were tentatively recognized in the *S. chilensis* complex in South America: *S. chilensis* and *S. microglossa*. Mid- and upper stem hair densities versus hair lengths for the specimens of the two species are plotted in Figure 2.

FIVE A PRIORI GROUPS ANALYSIS: TWO SOUTH AMERICAN AND THREE RELATED NORTH AMERICAN TAXA

A discriminant analysis was performed including all 160 specimens to determine which characters were most useful in separating the five species-level a priori groups: two South American, *Solidago chilensis* and *S. microglossa*, and three North American, *S. juliae*, *S. leavenworthii*, and *S. tortifolia*. The eight characters with highest F-values selected in a stepwise discriminant analysis were included in a complete discriminant analysis: ISTPUBD (stem hairs, number of hairs counted on 1 mm on the inflorescence stem), ULSERAT (stem hairs, number of hairs counted on 1 mm on the upper vegetative stem), CAPW (width of the inflorescence measured at the widest point [cm]), OPHYLL (outer phyllary length [mm] measured from the phyllary base to tip), RFLOR (number of ray florets per head), BSTPUBD (stem hairs, number of hairs counted on 1 mm on the basal stem), MLWID (mid-stem leaf width [cm], as measured from widest point to blade apex), and IPHYLV (inner phyllary number of veins) (Tables 1, 2) in decreasing order of discriminatory power. The F-matrix based on Mahalanobis distances between group centroids and associated probabilities indicate strong support for the five taxa (Table 3). All three tests for equality of group centroids (Wilks' lambda, Pillai's trace, and Hotelling-Lawley trace) indicated that the groups overall were significantly different (Table 4), and the null hypothesis that all groups were really the same was rejected. The F-values between *S. juliae* and *S. tortifolia* were the lowest, while values between *S. chilensis* and *S. tortifolia* were the highest.

Geisser a posteriori assignment probabilities were determined for each of the 160 specimens, and a classification matrix and a jackknifed classification matrix for these specimens were generated (Tables 5 and 6, respectively).

In the classificatory analysis, eight of the nine specimens assigned a priori to *Solidago juliae* were assigned a posteriori to that taxon. Five of these specimens had Geisser assignment probabilities between 93% and 100%, while the other three had assignment probabilities between 78% and 84%. One specimen assigned a priori as *S. juliae* was misclassified and assigned a posteriori very weakly to *S. leavenworthii* with Geisser assignment probabilities split among *S. leavenworthii* (42%), *S. juliae* (42%), and *S. tortifolia* (16%).

Of the 15 specimens assigned a priori to *Solidago leavenworthii*, 10 were assigned a posteriori to that taxon. Nine of the specimens had Geisser assignment probabilities between 99% and 100%, and one specimen had an assignment probability of 76%. Five of the specimens assigned a priori to *S. leavenworthii* were misclassified with assignment probabilities between 0% and 41% to the a priori group. Two of the specimens were placed a posteriori in *S. chilensis* (68% and 57% probabilities, respectively), and one specimen was placed in *S. juliae* (62% probability).

Table 2. Mean ± standard deviation and range (minimum–maximum) by species level for the a priori groups for the 45 traits included in the stepwise discriminant analysis of 160 specimens of *Solidago* subsect. *Triplinerviae*: *S. chilensis* Meyen, *S. microglossa* DC., *S. juliae* G. L. Nesom, *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott. See Table 1 for trait descriptions. N refers to the number of specimens scored for each species.

Trait	*S. chilensis*	*S. microglossa*	*S. juliae*	*S. leavenworthii*	*S. tortifolia*
	N = 88	N = 31	N = 11	N = 15	N = 15
STEMHT (cm)	64.8 ± 32.7	81 ± 28.3	95.2 ± 38.2	84.1 ± 29.2	83.3 ± 35.2
	7–170	36–167	60–180	47–165	30–140
ISTPUBD	3.8 ± 3.1	8.9 ± 2.3	14.8 ± 2.9	9.31 ± 3.2	11.5 ± 2.25
	2–16	2–22	11–27	3–20	6–21
USTPUBD	2.8 ± 2.65	8 ± 2.7	14.5 ± 2.7	5.3 ± 3	11 ± 2.5
	0–0	1–17	8–22	0–13	5–18
MSTPUBD	1.8 ± 2.2	6.7 ± 2.4	12.15 ± 4	3.05 ± 3	10.6 ± 2.5
	0–0	0–13	0–20	0–12	6–18
BSTPUBD	0.8 ± 1.8	4.6 ± 2.3	5.4 ± 5.4	0.4 ± 0.8	5.5 ± 4
	0–0	0–13	0–12	0–4	0–14
ISTHLN (mm)	0.2 ± 0.1	0.8 ± 0.2	0.5 ± 0.1	0.3 ± 0.1	0.3 ± 0.1
	0.06–0.75	0.21–1.5	0.19–0.75	0.21–0.5	0.19–0.67
USTHLN (mm)	0.2 ± 0.1	0.9 ± 0.15	0.5 ± 0.1	0.25 ± 0	0.3 ± 0.1
	0.06–1.25	0.21–1.67	0.21–0.94	0–0.37	0.19–0.67
MSTHLN (mm)	0.2 ± 0.1	0.9 ± 0.3	0.4 ± 0.2	0.2 ± 0.1	0.2 ± 0.1
	0.06–0.5	1.75–0.5	0.21–0.75	0–0.44	0.12–0.56
BSTHLN (mm)	0.1 ± 0.1	0.6 ± 0.3	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0
	0.06–0.75	0.21–1.25	0.12–0.5	0.06–0.5	0.12–0.44
MLLENG (mm)	61 ± 18	58.5 ± 18.2	50 ± 11.4	65.35 ± 19.8	40 ± 9.1
	3–130	22–105	27–88	26–103	25–65
MWID (mm)	6.6 ± 2.3	8.7 ± 3	7.2 ± 2.2	8 ± 1.9	5 ± 1.4
	0–32	4–19	4–17	4–13	2–8
MLWTOE (mm)	27.2 ± 9.1	27.1 ± 8.8	23.2 ± 5.5	31.7 ± 9.25	18.8 ± 4.5
	0–60	12–50	9–35	10–50	10–30
MSERAT	1.9 ± 2.4	2.7 ± 2	3.1 ± 4.5	7.2 ± 3.55	1.93 ± 0.8
	0–12	0–8	0–14	0–15	0–4
ULLENG (mm)	36.5 ± 12.3	30.4 ± 11	31 ± 10.5	37 ± 16.6	20.9 ± 8
	0.5–80	11–55	12–80	10–94	10–41
ULWID (mm)	3.95 ± 2.3	4.7 ± 1.7	4.6 ± 0.9	4.6 ± 1.7	3.1 ± 0.7
	0–27	1.5–10	2.5–9	2–10	1.5–5
ULWTOE (mm)	17.5 ± 6.3	15.6 ± 5.8	14.1 ± 3.5	18 ± 7.6	10.3 ± 3.95
	0–40	6–35	6–28	5–42	5–20
ULSERAT	0.5 ± 1.3	0.3 ± 0.6	0.9 ± 1.45	3.7 ± 2.8	0.7 ± 0.86
	0–10	0–5	0–6	0–13	0–4
ILLENG (mm)	18.65 ± 6.5	17.3 ± 5.5	18.05 ± 7.3	22.4 ± 8.5	12.2 ± 4.5
	4.4–45	6–40	8–40	5–43	4–30
ILWID (mm)	2.2 ± 1.5	2.8 ± 1	2.9 ± 1.2	3 ± 1.1	1.95 ± 0.5
	0.5–2.21	1–15	1–7	1–6	1–4
ILWTOE (mm)	8.95 ± 3.45	8.7 ± 3.3	8.6 ± 3.6	11.2 ± 4.5	6.1 ± 2.3
	1–25	3–27	4–20	2–29	2.5–14
ILSERAT	0.05 ± 0.3	0.01 ± 0.07	0.3 ± 0.8	1.15 ± 1.3	0.15 ± 0.4
	0–5	0–1	0–4	0–7	0–2
CAPBRANG	27.9 ± 9.85	29.8 ± 14.5	34.5 ± 5.3	27.9 ± 7.9	38.2 ± 6.1
	1–60	15–90	30–40	9–40	30–50
CAPW (cm)	12.0 ± 6.5	13.7 ± 6.5	21.7 ± 8.4	13.3 ± 6.7	15.4 ± 3.4
	1–30	3–27	11–37	2.5–29	9–21
CAPL (cm)	8.7 ± 6.6	8.8 ± 4.8	8.3 ± 1.7	6.8 ± 5.0	9.4 ± 3.6
	2–35	2–18	5.5–1	1.5–20	3–15
LONGBR (cm)	5.5 ± 4.5	5.1 ± 3	7.3 ± 3.4	6.3 ± 6.2	6 ± 2.25
	2–35	1–12	3.5–12	1.5–20	2–10
INVOLHT (mm)	4.4 ± 0.5	4.4 ± 0.4	3.4 ± 0.25	4.3 ± 0.6	3.1 ± 0.2
	3–7	3–6	4.1–2.6	2.9–6	2.6–4
OPHYLL (mm)	1.8 ± 0.2	1.7 ± 0.2	2.6 ± 4.1	1.6 ± 0.3	1.1 ± 0.1
	1.1–2.7	0.17–2.6	0.8–3	1–2.6	0.7–1.6

Table 2. Continued.

Trait	*S. chilensis*	*S. microglossa*	*S. juliae*	*S. leavenworthii*	*S. tortifolia*
OPHYLW (mm)	0.55 ± 0.1	0.5 ± 0.05	0.5 ± 0.2	0.6 ± 0.1	0.3 ± 0
	0.3–1.6	0.3–0.7	0.3–1.3	0.4–0.8	0.2–0.6
OPHYLWTOE (mm)	1.3 ± 0.2	1.3 ± 0.15	1 ± 0.2	1.2 ± 0.3	0.7 ± 0.2
	0.5–2.2	0.8–1.8	0.4–1.3	0.6–2.1	0.3–1.3
OPHYLV	1.1 ± 0.2	1.05 ± 0.2	1 ± 0	1 ± 0	0 ± 1
	1–3	1–3	1–1	1–1	1–1
IPHYLL (mm)	3.8 ± 0.4	3.8 ± 0.35	2.8 ± 0.2	3.5 ± 0.5	2.6 ± 0.3
	2.4–5.1	0.29–4.8	2.3–3.5	2.6–5	1.9–3.6
IPHYLW (mm)	0.6 ± 0.1	0.6 ± 0.1	0.55 ± 0.05	0.7 ± 0.1	0.49 ± 0.1
	0.3–1	0.3–0.8	0.4–0.7	0.5–1	0.3–0.8
IPHYLWTOE (mm)	1.9 ± 0.2	1.8 ± 0.2	1.4 ± 0.1	1.7 ± 0.3	1.3 ± 0.2
	0.9–2.6	1–2.4	0.8–1.7	0.1–2.9	0.9–2
IPHYLV	1.9 ± 0.7	2.3 ± 0.7	1.7 ± 0.6	1.7 ± 0.8	1.25 ± 0.4
	1–7	1–3	1–3	1–3	1–3
DFLOR	13.5 ± 3.1	15.1 ± 3.6	10.4 ± 1.8	11.7 ± 4.5	4.75 ± 1.2
	7–29	4–28	6–18	7–29	2–8
RSTRAPL (mm)	2.9 ± 7.8	1.9 ± 0.3	1.3 ± 0.25	1.9 ± 0.4	1.35 ± 0.35
	0.4–3.1	1–2.9	0.7–1.8	1–3	0.7–4
RSTRAPWD (mm)	0.5 ± 0.7	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1
	0.1–0.9	0.1–0.7	0.1–0.6	0.2–0.8	0.1–1.5
RACHBL (mm)	1.1 ± 3.7	0.8 ± 0.6	0.8 ± 0.2	0.8 ± 0.2	0.6 ± 0.2
	0.3–3.3	0.4–4	0.5–1.3	0–1.5	0.4–1.2
RPAPL (mm)	3.4 ± 0.5	3.1 ± 0.6	2.2 ± 0.45	2.95 ± 0.9	2.2 ± 0.2
	2.3–4.5	0.37–4.3	1–3	0.32–4.3	1.6–2.8
#DFLOR	9.2 ± 3.2	8 ± 1.85	5.8 ± 1	8.05 ± 5	3.6 ± 0.9
	2–25	2–30	2–7	4–30	1–6
DCORL (mm)	3.7 ± 0.4	3.6 ± 0.3	3.2 ± 0.2	3.8 ± 0.4	2.8 ± 0.3
	2.4–4.9	2.7–4.6	2.5–4	2.6–4.7	0.3–3.8
DACHBL (mm)	0.8 ± 0.2	0.8 ± 0.1	0.85 ± 0.2	0.8 ± 0.2	0.6 ± 0.2
	0.1–2.6	0.5–1.2	0.5–1.3	0.5–1.2	0.4–1.3
DCORLIMB (mm)	2.6 ± 0.4	2.5 ± 0.3	2 ± 0.15	2.5 ± 0.3	1.9 ± 0.2
	1.5–4.6	1.4–3.5	1.5–2.5	1.7–3.5	1.3–2.5
DLOBL (mm)	2 ± 0.3	1.05 ± 0.2	1.1 ± 0.3	1 ± 0.1	0.8 ± 0.3
	0.12–3.9	0.6–2.3	0.4–2.7	0.7–1.5	0.4–1.9
DPAPL (mm)	3.6 ± 0.5	3.4 ± 0.4	2.6 ± 0.3	3.5 ± 0.5	2.2 ± 0.5
	0.8–5.1	2.3–4.4	2–3.1	2.1–4.4	0.5–3

All 14 specimens assigned a priori to *Solidago tortifolia* were assigned a posteriori to that taxon. Eleven of the specimens were classified with probabilities of 92%–100%; one was classified with only 63% probability to *S. tortifolia* and 37% to *S. juliae*.

Of the 88 specimens assigned a priori to *Solidago chilensis*, 77 were assigned a posteriori to that taxon, with 60 specimens having Geisser assignment probabilities between 91% and 100% and 17 specimens having assignment probabilities between 62% and 88% (two specimens with less than 75% from Jujuy, Argentina). Seven of the misclassified specimens were assigned to *S. microglossa* with Geisser assignment probabilities between 51% and 98% (from Jujuy, Río Muerto [Chaco], Salta, and Tucuman, Argentina, and Cochabamba, Licoma, and Santa Cruz, Bolivia), and three were assigned to *S. leavenworthii* with probabilities between 99% and 100% (from Jujuy, Salta, and San Luis States in Argentina). One was placed in *S. juliae* with 77% probability (from Santa Cruz, Bolivia).

Of the 30 specimens assigned a priori to *Solidago microglossa*, 28 were assigned a posteriori to that taxa. Nineteen of the specimens were assigned with 90%–100% probability to *S. microglossa*; nine were assigned with 51%–89% probability. Two specimens were assigned a posteriori to *S. chilensis*, with 60% and 86% probability (from Formosa, Argentina, and Central Department, Paraguay, respectively).

A canonical analysis was performed, and the canonical variant scores on the first and second and on the first and third canonical axes (CAN 1, CAN 2, and CAN 3) were plotted for the five putative taxa

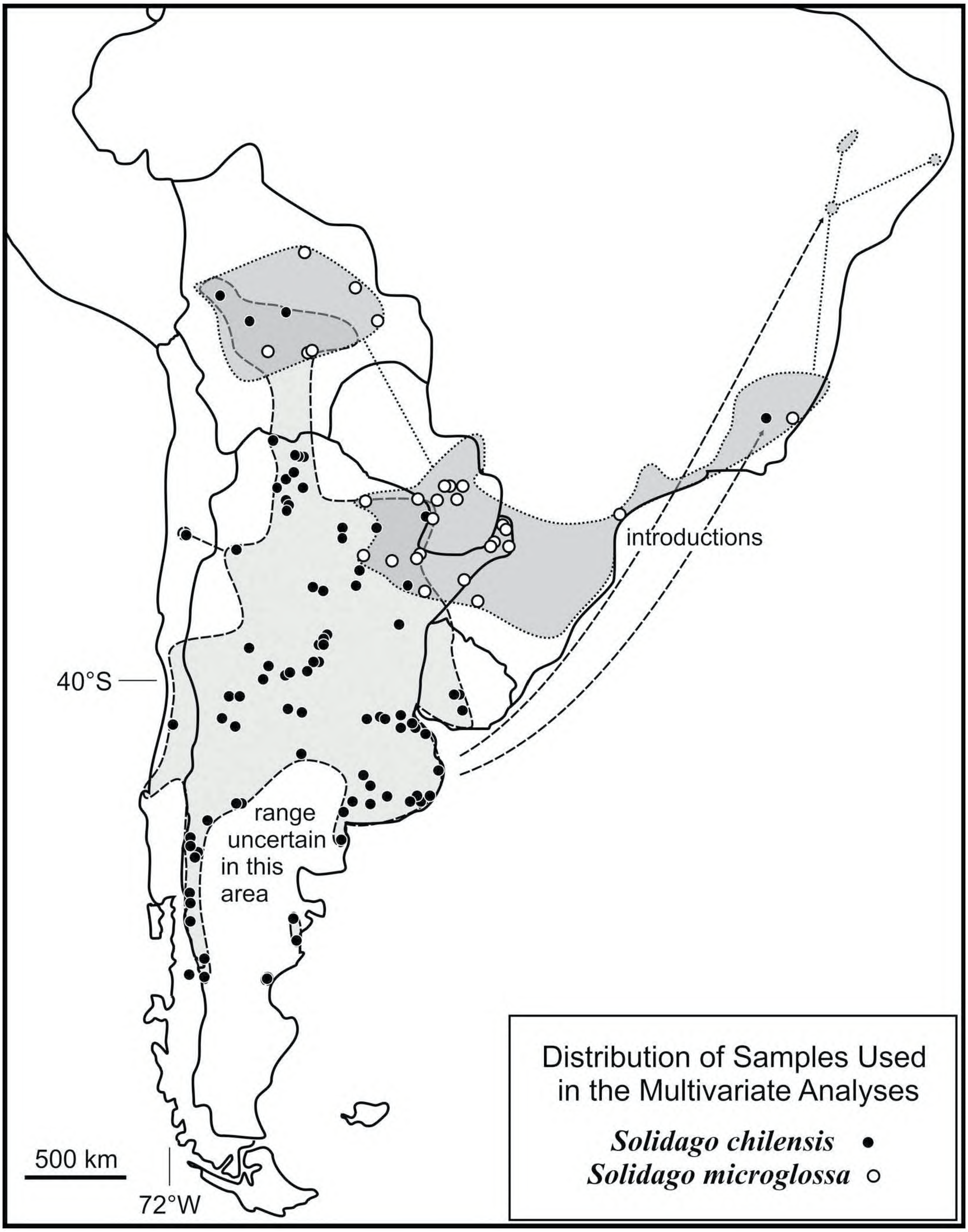
Distribution of Samples Used in the Multivariate Analyses
Solidago chilensis ●
Solidago microglossa ○
introductions
range uncertain in this area
40°S
72°W
500 km

Figure 1. Distribution in South America of 116 specimens of *Solidago chilensis* (black dots) and 33 specimens of *S. microglossa* (white dots). The location of a specimen from Madeira Island, Portugal, is not shown. Shaded areas indicate the ranges of distribution based on Lopez Laphitz (2009).

studied (Fig. 2; 95% confidence ellipses included). The eigenvalue for the first canonical variate (3.121) accounted for 87.5% of the variation, the second (1.560) for 11.2%, and the third (0.666) for an additional 1.3%.

CHROMOSOME COUNTS

Chromosome numbers were determined for 27 plants grown from field-collected cypselae at the University of Waterloo Department of Biology green-

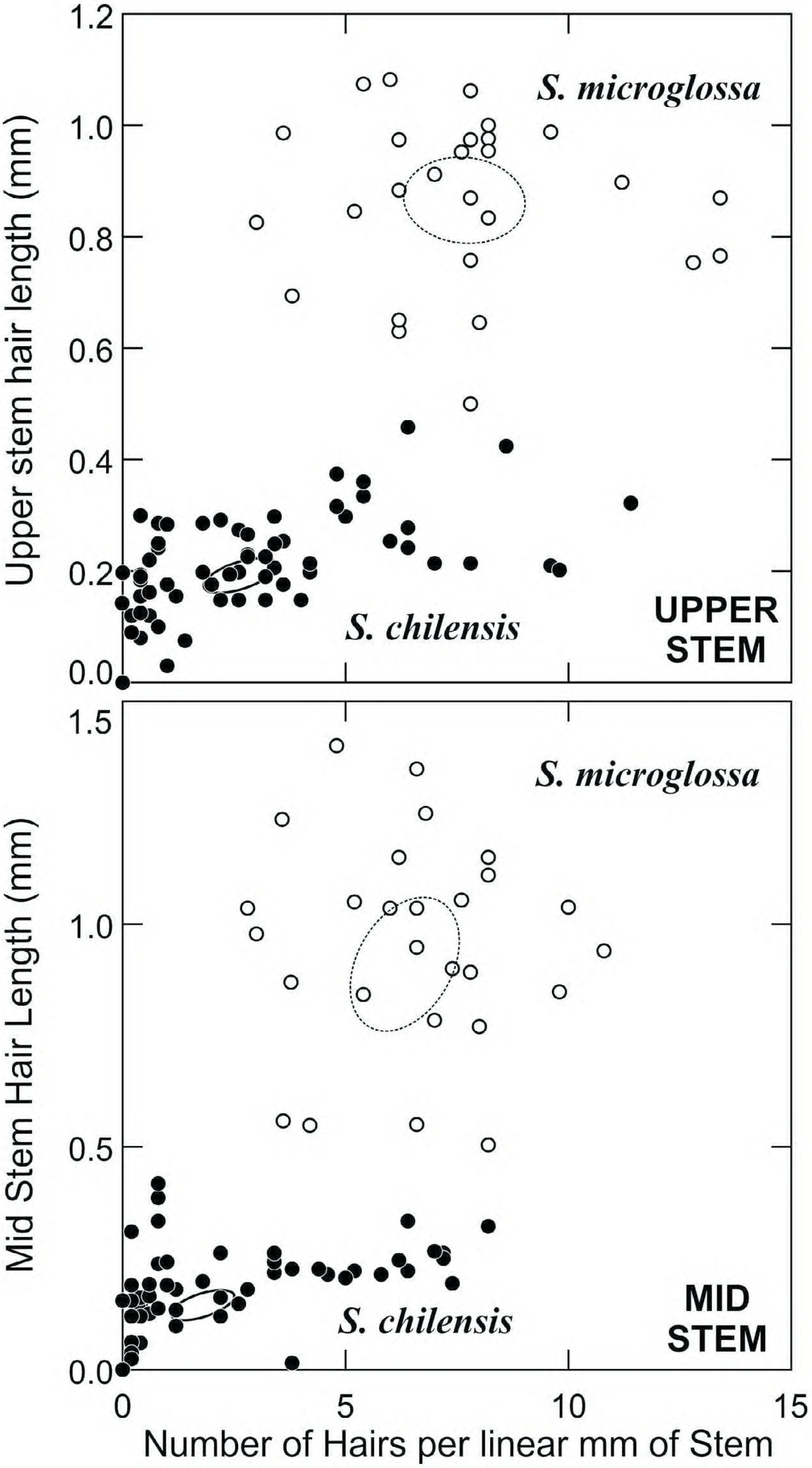

Figure 2. Scatterplots of length of hairs (mm) versus the number of hairs per mm of mid- and upper stems for specimens of *Solidago chilensis* (dots) and *S. microglossa* (circles).

Table 3. F-statistics $F_{0.05}$ and associated null hypothesis probabilities among the five putative taxa; $P < 0.0000$ in all cases; *Solidago chilensis* Meyen, *S. microglossa* DC., *S. juliae* G. L. Nesom, *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott.

	S. microglossa	*S. chilensis*	*S. juliae*	*S. leavenworthii*
S. chilensis	17.633			
S. juliae	14.191	27.430		
S. leavenworthii	17.704	16.336	12.818	
S. tortifolia	29.805	40.429	4.446	16.694

Table 4. Multivariate statistics and F-approximations for the Wilks' lambda, Pillai's trace, and Hotelling-Lawley trace tests from the discriminant analysis of the five species-level groups: *Solidago chilensis* Meyen, *S. microglossa* DC., *S. juliae* G. L. Nesom, *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott.

	Value	F-values	DF	*P* tail
Wilks' lambda	0.060	18.094	32, 532	0.0000
Pillai's trace	1.716	13.799	32, 588	0.0000
Hotelling-Lawley trace	5.022	22.364	32, 570	0.0000

house (Appendix 1). All counts were diploid $2n = 18$; 21 for *Solidago chilensis* from Argentina and Chile and six counts for *S. microglossa* from Argentina.

DISCUSSION

SOLIDAGO IN SOUTH AMERICA

Based on univariate and discriminant analyses and observations on plants in the field and greenhouse, two native species of *Solidago* subsect. *Triplinerviae* should be recognized in South America: *S. chilensis* and *S. microglossa*. The nomenclature was chosen after observations were made on type specimens and available high-resolution photographs of the type specimens (Lopez Laphitz, 2009). The character found most reliable in separating the two taxa was stem hair length. Other traits used in the literature to separate species or varieties of South American goldenrods did not yield groups that were as statistically well supported or had high numbers of specimens with low probabilities of placement into the a priori groups.

Observations of plants grown in the greenhouse clearly showed that hair length was an inheritable character and a trait little influenced by environmental conditions. The selection pressures favoring short versus long hairs and differences in hair densities are unknown. Hair density is variable in *Solidago* subsect. *Triplinerviae* and the variation in hair density in *S. chilensis* is similar to that seen in *S. lepida* of North America (Semple et al., 2013). The complete lack of hairs on the stem is an extreme condition in *S. chilensis* as is clear in Figure 2. Published keys in Cabrera (1974) and Sancho and Viera Barreto (2014) separating glabrous (*S. chilensis* var. *chilensis*) and pubescent (*S. chilensis* var. *megapotamica*) races of a single species, *S. chilensis* s.l., do not account for the large number of specimens of *S. chilensis*, as delimited here with statistical support, that have some hairs on the midstem or just the upper stem and in the inflorescence. Hair length is critical in separating the two species *S. chilensis* and *S. microglossa* (synonym, *S. chilensis* var. *megapotamica*) used in conjunction with several other traits (e.g., mid-stem leaf width, numbers of ray florets; see Key to Species below).

In contrast, the inflorescence density character used in the published floristic keys (Cabrera, 1971; Sancho & Espinar, 2003) could be affected by different environmental factors (Jakobs et al., 2004) and is based on a misapplication of the name *Solidago patagonica*. The type specimen of *S. patagonica* Phil. (*Cox s.n.*, SGO, digital image!) was determined to be a member of *S. chilensis*, and the name belongs in synonymy. Sancho and Viera Barreto (2014) noted that the inflorescence density difference really applies to a non-native escaped cultivar collection of *S. virgaurea*, native to Europe. Lopez Laphitz (2009) first noted this fact.

A member of *Solidago* subsect. *Junceae* was reported from South America for the first time and identified as *S. missouriensis*-like in Lopez Laphitz (2009) and subsequently described as *S. argentinensis* Lopez Laphitz & Semple (Lopez Laphitz et al., 2011). Comparison of the South American specimens with multiple species of North American *Solidago* subsect. *Junceae* confirmed that South American plants fit well within the description of the subsection in Semple and Cook (2006), with some variations such as phyllaries sometimes with multiple veins and often minutely glandular. A multivariate morphometric study of North and South American members of subsection *Junceae* was conducted by Lopez Laphitz et al. (2011). Sancho and Viera Barreto (2014) included *S. argentinensis* in their floristic treatment.

SOLIDAGO SUBSECT. *TRIPLINERVIAE* IN SOUTH AMERICA AND RELATED TAXA IN NORTH AMERICA

The discriminant analysis including *Solidago chilensis* and *S. microglossa* from South America and *S. juliae*, *S. leavenworthii*, and *S. tortifolia* from North America provided strong support for recognizing all five a priori groups. The null hypothesis was rejected and five species-level groups accepted. The South American *Solidago* specimens were as differ-

Table 5. Classification matrix obtained by classificatory discriminant analysis of the five putative taxa: *Solidago chilensis* Meyen, *S. microglossa* DC., *S. juliae* G. L. Nesom, *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott. Rows show number of specimens in an a priori group assigned to each a posteriori group and the percent of specimens in an a priori assigned a posteriori to the a priori group.

	A posteriori					
A priori	*S. microglossa*	*S. chilensis*	*S. juliae*	*S. leavenworthii*	*S. tortifolia*	% correct
S. microglossa	28	2	0	0	0	93%
S. chilensis	7	77	1	3	0	88%
S. juliae	0	0	8	1	0	89%
S. leavenworthii	1	3	1	10	0	67%
S. tortifolia	0	0	0	0	14	100%
Totals/Mean	36	82	10	14	14	88%

ent from the three North American taxa as these three species were different from each other. Although the analysis showed five well-separated groups, classificatory analyses showed that some specimens of *S. leavenworthii*, *S. chilensis*, and *S. microglossa* had weak support for placement a posteriori in their a priori group or were misclassified. For instance, 11 specimens identified a priori as *S. chilensis* were misclassified; three were placed a posteriori in *S. leavenworthii*, seven in *S. microglossa*, and one in *S. juliae*. These specimens were re-examined, and they showed ambivalent morphological characteristics (problematic specimens), such as longer than usual hairs for *S. chilensis* in contrast to the a priori classification that defined *S. chilensis* as short-haired plants. Furthermore, these problematic specimens were restricted to two geographical areas: (1) the northwestern portion of the range in South America, including Bolivia and northern Argentina, and (2) northeastern Argentina in the provinces of Corrientes and Formosa. Because these ambivalent morphological traits were restricted to two geographic areas, three hypotheses were suggested to account for the a posteriori assignments of *S. chilensis* specimens to other species. First, Bolivia and adjacent areas are postulated as the probable starting point for the location of the original introduction from North America (possibly from northern Mexico) with subsequent unknown evolutionary pressures resulting in differentiation into two well-defined, mostly allopatric taxa occupying different habitats. Second, both geographic areas are tentatively suggested as zones of potential interspecific hybridization due to more recently occurring sympatry; this applies to the *S. chilensis* specimens assigned a posteriori to *S. microglossa*. Lopez Laphitz (2009) and Gonçalves Silva et al. (2009) provided evidence of human-aided, long-distance dispersal of *S. chilensis* into equatorial Brazil, the West Indies, and the Madeira Islands off the coast of Africa. Human-aided dispersal of *S. microglossa* in South America also seems likely. Third, local variation in some traits in *S. chilensis* resulted in several pockets of somewhat divergent populations that happened to be more similar to North American species; the specimens were correctly placed a priori in *S. chilensis*, but were atypical for the species. The a posteriori assignments to *S. juliae* and *S. leavenworthii* on technical traits should not be taken as evidence that these two North American species are present in South America because the specimens had the traits used to assign them a priori into the *S. chilensis* group.

Table 6. Jackknifed classification matrix obtained by classificatory discriminant analysis of the five putative species: *Solidago chilensis* Meyen, *S. microglossa* DC., *S. juliae* G. L. Nesom, *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott. Rows show number of specimens in an a priori group assigned to each a posteriori group and the percent of specimens in each a priori group assigned a posteriori to the a priori group.

Group	A posteriori					
A priori	*S. microglossa*	*S. chilensis*	*S. juliae*	*S. leavenworthii*	*S. tortifolia*	% correct
S. microglossa	28	2	0	0	0	93%
S. chilensis	8	76	1	3	0	86%
S. juliae	0	0	6	1	2	67%
S. leavenworthii	1	3	1	10	0	67%
S. tortifolia	0	0	1	0	13	100%
Totals/Mean	37	81	9	14	15	88%

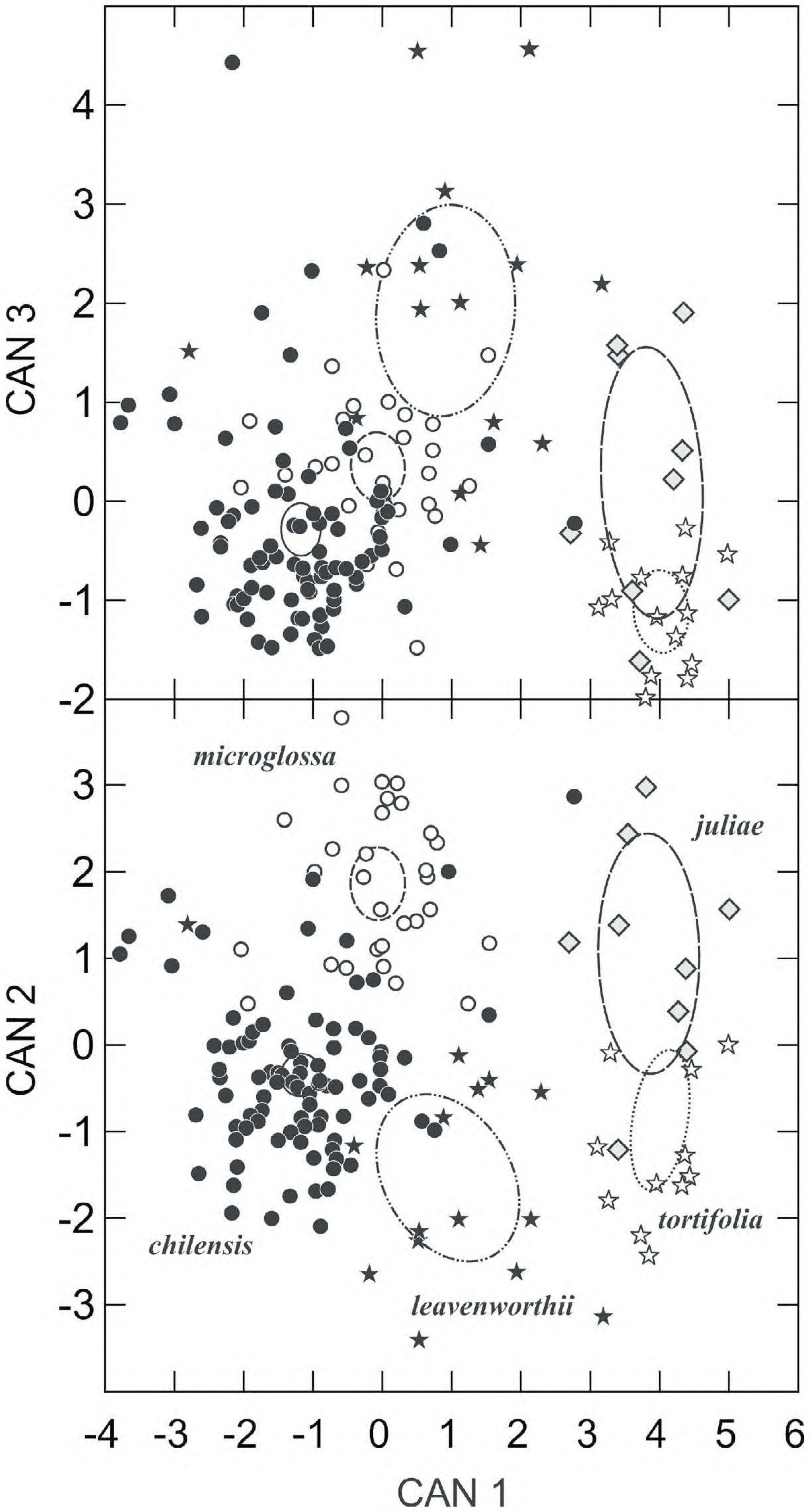

Figure 3. Scatterplots of the first and second (bottom) and the first and third (top) canonical scores (CAN 1, CAN 2, CAN 3) for five species-level groups with 95% confidence intervals indicated for each group by broken lines. *Solidago chilensis* is represented by solid dots and solid line ellipses, *S. juliae* by shaded diamonds and short broken line ellipses, *S. leavenworthii* by solid stars and dash-dot ellipses, *S. microglossa* by open circles and long dash ellipses, and *S. tortifolia* by open stars and dotted line ellipses.

The origins of *Solidago* in South America have not been studied in detail. However, the presence of North American taxa in central and southern South America could be a result of island hopping down the cordillera via similar habitats that no longer exist in Central America and northern South America or the result of long-distance transport of the fruit propagules attached to the feathers of migrating birds. Alan Graham (pers. comm.) suggested the latter is much more likely as there is little evidence for the existence of intermediate, temporary habitats similar to those found in northern Mexico and Bolivia today. Evidence of recent long-distance dispersal of *S. chilensis* to locations in the Northern Hemisphere, e.g., Puerto Rico in the West Indies (Lopez Laphitz, 2009) and Madeira Island off the coast of Africa (Gonçalvez Silva et al., 2009), clearly shows that long distance is not a barrier to migration and colonization by members of *Solidago* subsect. *Triplinerviae*. Also, the North American *S. altissima*, a relative of *S. chilensis* in subsection *Triplinerviae*, has naturalized in eastern China, Taiwan, and Japan (Chen & Semple, 2011).

Results also suggest that the three morphologically similar species from southern North America included in the discriminant analyses and the two species from South America possibly shared a common ancestor in the Pleistocene, and all five species are relatively recently evolved by the same processes of founder effect, isolation, and adaptation. The times of divergences are speculative, but advances and retreats of glaciers would have provided a strong stimulus for expansion and contraction of ranges in North America and Canada. *Solidago altiplanities*, native to the southern High Plains of Texas and Oklahoma, is also morphologically similar to the five species analyzed in this study and may have diverged from a common ancestor during earlier glacial peak and contraction events. Of note is the fact that only in South America did the plesiomorphic short, dense stem pubescence of the putative ancestral taxon evolve into both nearly glabrous and longer-haired conditions found separately in the two South American species. In North America, the three species remained short haired and generally densely so. Only in *S. leavenworthii*, the only known polyploid species in the complex, did North American plants approach the glabrous/glabrate condition seen in the extreme in some plants in *S. chilensis* in South America. *Solidago altissima* also has similar hairy stems and may be related to these species, although it has morphological affinities (Semple et al., 2015) with other species of *Solidago* subsect. *Triplinerviae* as well, making its phylogenetic position uncertain within the subsection.

Interspecific hybridization is common among *Solidago* species in North America (Semple et al., 1999), and it should not be excluded as a possible explanation for the presence of specimens with ambivalent identity in South America. For instance, observations on this study of somewhat longer hairs in specimens classified a posteriori as *S. chilensis* showed possible evidence of hybridization with longer haired *S. microglossa*. However, this hypothesis was not tested with experimental crosses between *S. chilensis* and *S. microglossa*. Semple and Semple (1977) noted that there was a greater variability in morphological characteristics of hybrids than expected from parental species. Therefore, similar variability might be seen in the wild hybrid swarms including some of the misclassified specimens. Further work is needed to document the presence of *S. chilensis* × *S. microglossa* hybrids in Bolivia and northern Argentina.

DISTRIBUTION AND CYTOGEOGRAPHY OF *SOLIDAGO* SUBSECT. *TRIPLINERVIAE* IN SOUTH AMERICA

In total, 32 diploid ($2n = 18$) chromosome number determinations for populations of *Solidago chilensis* and *S. microglossa* have been reported either here (Appendix 1) or previously (Covas & Schnack, 1946, 1947; Turner et al., 1979; Hunzinker et al., 1989; Dematteis et al., 2007). The ranges of distributions of *S. chilensis* and *S. microglossa* and the distribution of cytological samples are shown in Figure 4. The new counts are in agreement with previous reports listed under various species and variety names. Although some obviously larger-headed individuals from South America were included in the multivariate analyses, the variation cannot be explained by polyploidy. In contrast, in North America, polyploidy is common in most species of *Solidago* subsect. *Triplinerviae* (Semple et al., 1984; Semple & Cook, 2006). In other parts of the world, it is typically the polyploids of species of subsection *Triplinerviae* that have successfully naturalized, e.g., *S. gigantea* Aiton (Schlaepfer et al., 2008a, 2008b, 2010) and *S. altissima* (Chen & Semple, 2011). Of note, the putative close relatives of *S. chilensis* and *S. microglossa* in North America (*S. juliae*, *S. tortifolia*, and *S. altiplanities*) are all known only at the diploid level, but sample sizes are very small. Additional work on the cytogeography of the South American species is needed to sample all parts of the range in addition to those indicated in Figure 4.

TAXONOMIC TREATMENT OF *SOLIDAGO* IN SOUTH AMERICA

I. Solidago L., Sp. Pl. 2: 878. 1753. TYPE: *Solidago virgaurea* L. (lectotype, designated by Britton & A. Brown, Ill. Fl. N. US, ed. 2(3): 380. 1913.

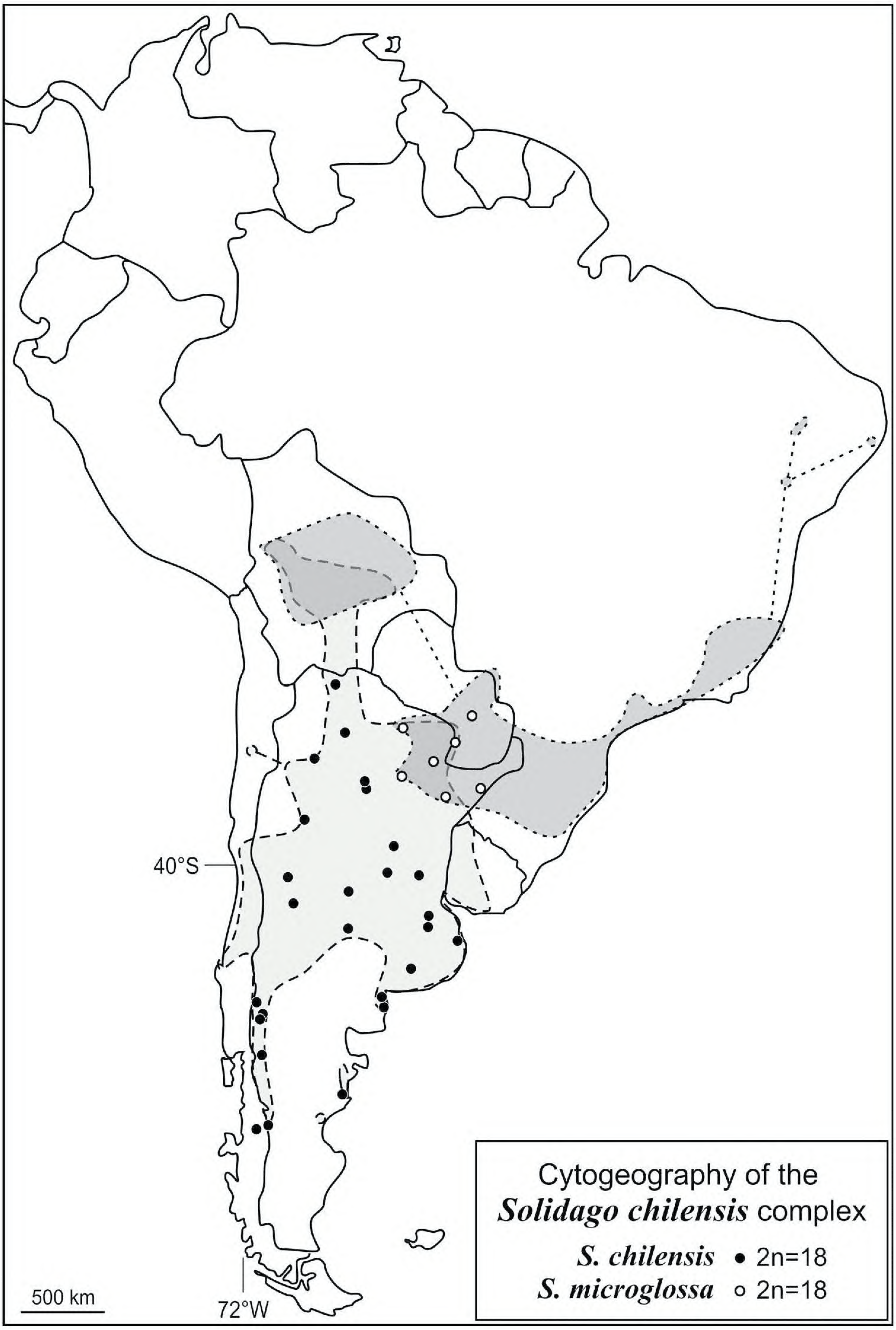

Figure 4. Cytogeographic map of *Solidago chilensis* (black dots) and *S. microglossa* (white dots) in South America based on chromosome counts reported herein and from the literature.

KEY TO *SOLIDAGO* IN SOUTH AMERICA

1. Basal rosettes usually present at time of flowering; rosette and basal stem leaves the largest, pairs of small lateral branch leaves often present in axes of upper stem leaves; stems proximally glabrous, sparsely strigose distally; involucres 3.5–5.5 mm high, phyllaries ovate, linear-ovate, or oblong … *S. argentinensis* Lopez Laphitz & Semple (2).

1′. Basal rosettes not present at time of flowering; lower part of the mid-stem leaves largest or lowest stem leaves largest and stems pubescent; stem pubescence to glabrate; involucres 3.5–10 mm high, phyllaries broadly to narrowly lanceolate.

  2. Inflorescence lax; involucres 6–10 mm; basal leaves the largest; stem leaves relatively few; not triple-nerved, stems glabrate; not native .... *S. virgaurea* L. (1).

  2′. Inflorescence congested; involucres 3.5–5.5 mm high at anthesis; lower part of the mid-stem leaves the largest; stem leaves many, triple-nerved; stems glabrate, canescent or short villose; native.

    3. Stem hairs short, 0.1–0.4 mm long; stem pubescent to glabrate .... *S. chilensis* Meyen (3).

    3′. Stem hairs 0.4–1.2 mm long; stems hispid-villose .... *S. microglossa* DC. (4).

Ia. Solidago subsect. **Solidago.**

Leaves basal, often present in rosettes at flowering; proximal-most cauline leaves petiolate to attenuate-subpetiolate, sometimes present at flowering, largest, distal reduced. Heads in racemiform, paniculiform arrays, sometimes corymbiform, wand- to club-shaped, branches ascending. Phyllaries usually not striate, glabrous to strigose, eglandular to sparsely glandular, lanceolate. Pappus bristles usually in 2 series, the inner series longest, somewhat to moderately clavate.

Included species. (Ca. 11 native to Eurasia and arctic and alpine North America) *Solidago dahurica* (Kitag.) Kitag. ex Juz., *S. decurrens* Lour., *S. kurilensis* Juz., *S. leiocarpa* DC., *S. litoralis* Savi, *S. minutissima* (Makino) Kitam., *S. multiradiata* Aiton, *S. nipponica* Semple, *S. pacifica* Juz., *S. spithamaea* M. A. Curtis ex A. Gray, and *S. virgaurea*.

1. Solidago virgaurea L., Sp. Pl. 880. 1753. TYPE: "Habitat in Europe pascuis siccis," *Herb. Linnaeus 998.15* (lectotype, designated by Garbari & Cecchi in Jarvis & Turland, 1998: 368, LINN 998.15!).

Syntypes. Solidago 3, *Clifford 409* (BM), Solidago 3a, *Clifford 409* (BM), Solidago 3b, fol. A, *Clifford 409*, Solidago 3b, fol. B, *Clifford 409* (BM), Solidago 3e, *Clifford 409* (BM); Herb. Burser XV: 66 (UPS).

Herbaceous perennials from short rhizomes; stems erect, 13.5–110 cm tall, glabrate below to sparsely to densely strigose distally. Leaves basal and proximal obovate to oblanceolate, often present at flowering, in most of the cases the biggest on the plant, petiolate, 4.5–21.1 × 0.9–4.2 cm, blades lanceolate to oblanceolate, abaxial and adaxial faces glabrous or sparsely strigose, abaxial veins sometimes densely strigose, margins serrate, ciliate; mid-stem leaves lanceolate to narrowly lanceolate, sessile, bases tapering, 3.5–11.2 cm, serrations 0 to 14; distal lanceolate to linear-lanceolate, reduced upward, 2–9.3 × 0.4–2.4 cm, serrations 0 to 9. Heads racemiform to thyrsiform-paniculiform arrays, congested and few-headed in short plants to lax in taller plants with longer branches and peduncles, branches ascending, sparsely to densely strigose. Involucres campanulate, 4.8–8 mm high at flowering, larger with age; phyllaries in 3 or 4 imbricate series, those of outer series ovate to lanceolate, middle lanceolate, 2.3–5.4 × 0.6–1.5 mm, apex tapering, with inner phyllaries oblanceolate to linear-lanceolate. Ray florets 1 to 10; laminae yellow, 2.9–7 × 0.5–2.1 mm; disk florets 1 to 29, averaging 13; corollas 4.1–6.9 mm, lobes 0.35–1.8 mm. Cypselae obconic to linear obconic, very sparsely to densely strigose over the entire body, body length at anthesis, 0.8–2.0 mm, to 3 mm at maturity; longest pappus bristles 3.6–6.4 mm. Chromosome count $2n = 18$. (Description based on European collections.)

Phenology. Solidago virgaurea has been observed as flowering in March in South America.

Habitat and distribution. Solidago virgaurea is known from one collection, *Cabrera 5015* (LP), from Rio Negro, Argentina. The species is native mainly to Europe and to Morocco and Pakistan, India, and Nepal (and possibly adjacent Tibet in China) in the mountains.

Ib. Solidago subsect. **Junceae** (Rydb.) G. L. Nesom, Phytologia 75: 11. 1993. *Solidago* [sp. group] *Junceae* Rydb., Fl. Plains N. Amer. 792. 1932. *Solidago* ser. *Junceae* (Rydb.) G. L. Nesom, Phytologia 75: 9. 1993. TYPE: *Solidago juncea* Aiton.

Leaves basal, often present in rosettes at flowering, proximal-most cauline petiolate to attenuate-subpetiolate, sometimes present at flowering, largest; cauline sometimes 3-nerved (with 2 prominent lateral nerves), distal usually subtending fascicles of small linear leaves of lateral branches, 2 usually much larger than others. Heads in thyrsiform-paniculiform arrays, wand- to club-shaped or sometimes secund and cone-shaped, proximal branches ascending to spreading; phyllaries usually not striate, glabrous to strigose, eglandular to sparsely glandular. Pappus bristles usually in 2 series, inner series weakly, if at all, clavate (modified from Semple & Cook, 2006).

Included species. (Nine, North America, northern Mexico; South America, Argentina, Bolivia.) *Solidago argentinensis* Lopez Laphiz & Semple, *S. confinis* A. Gray, *S. durangensis* G. L. Nesom, *S. gattingeri* Chapm. ex A. Gray, *S. guiradonis* A. Gray, *S. juncea* Aiton, *S. missouriensis*, *S. pinetorum* Small, and *S. spectabilis* (D. C. Eaton) A. Gray.

2. Solidago argentinensis Lopez Laphitz & Semple, Novon 21(2): 223. 2011. TYPE: Argentina. Mendoza: Dpto. San Rafael, Rio Salado Superior entre, 29 Jan. 1966, *Ruiz Leal 24529* (holotype, LP!).

Herbaceous perennials from short to long rhizomes; stems erect, 18–50 cm tall, glabrate at base, with increasing hair density distally, strigulose. Basal cauline leaves sometimes present at flowering and relatively large; mid- to distal cauline leaves much reduced distally; often subtending clusters (fascicles) of small lateral branch leaves; lower stem leaves petiolate, 20–80 mm including petiole, 3–14 mm wide, margins serrations 0 to 7; mid-stem leaves sessile, rapidly reduced upward, oblanceolate to lanceolate, 25–65 × 3–12 mm, margins serrations 0 to 5; upper and inflorescence stem leaves sessile, reduced, lanceolate to linear, 12–58 × 0.5–5 mm. Heads paniculiform (pyramidal), nodding or secund, 5–21 × 2–6 cm; involucres 3.5–5.5 mm high; phyllaries in 3 or 4 series, those of the outer series ovate, with the inner phyllaries linear-ovate to oblong. Ray florets 6 to 19, strap 1–3 × 0.2–0.7 mm; disk florets 5 to 19, corollas 3–4.8 mm, lobes 0.6–1.5 mm. Cypsellae obconic, 0.5–1.2 mm; pappus bristles 3.2–5 mm. Chromosome number unknown.

Phenology. *Solidago argentinensis* has been collected in flower from January to early March.

Habitat and distribution. *Solidago argentinensis* is known from Patagonia in Argentina and to the north (Chubut, Mendoza, Neuquen, and Rio Negro Provinces). It has been collected from Juncal, Chile, and Valle de Cochabamba, Bolivia.

Ic. Solidago subsect. **Triplinerviae** (Torr. & A. Gray) G. L. Nesom, Phytologia 75(1): 8. 1993. Basionym: *Solidago* [unranked] *Triplineriae* Torr. & A. Gray, Fl. N. Amer. 2(2): 222. 1842. TYPE: *Solidago canadensis* L. (lectotype, designated by Nesom, 1993: 8).

Leaves with basal rosettes absent; proximal cauline leaves nearly always withering by flowering, sessile, proximal, most not as large as lower mid-stem leaves and sometimes distal, 3-nerved (2 lateral nerves prominent, sometimes obscurely so and only on proximal leaves). Heads in thyrsiform-paniculiform arrays, usually congested cone-shaped (pyramidal), secund, sometimes leafy arrays (club-shaped in *Solidago elongata*), proximal branches often arching, secund, branches sometimes shorter than subtending leaves; phyllaries usually not striate, sometimes minutely stipitate-glandular. Pappus bristles usually in 2 series, the series sometimes similar, inner usually weakly if at all clavate, rarely moderately so (modified from Semple & Cook, 2006).

Included species. (Ca. 16, 11 in the flora, from North America, South America; introduced in Eurasia, Africa, Oceania). *Solidago altissima*, *S. altiplanities*, *S. brendiae*, *S. canadensis*, *S. chilensis*, *S. elongata*, *S. fallax*, *S. gigantea*, *S. gypsophila* G. L. Nesom, *S. juliae*, *S. leavenworthii*, *S. lepida*, *S. microglossa*, *S. muelleri* Standl., *S. pringlei* Fernald, *S. rupestris* Raf., *S. shortii* Torr. & A. Gray, and *S. tortifolia*.

3. Solidago chilensis Meyen, Reise Erde 1: 311. 1834. TYPE: Chile. "in campus chilesibus," de Chile y Pampas (in sched. label), s.d., *Née s.n.* (holotype, B†; neotype, designated here, G-DC!, photo G-DC010427_1!).

Solidago linearifolia DC., Prodr. [de Candolle] 5: 341. 1836. *Solidago microglossa* DC. var. *linearifolia* (DC.) Baker in Martius, Fl. Bras. 6(3): 10. 1882. TYPE: Chile. "in campus Chilensibus," s.d., *Née s.n.* (holotype, G-DC!).

Solidago coquimbana Phil., Linnaea 33: 138. 1864–1865. TYPE: Chile. Cordera: Cordillera de Thapel, Jan. 1860, *Volikmann s.n.* (holotype, SGO not seen, photo!).

Solidago laxiflora Phil., Anales Univ. Chile 87: 429. 1894. TYPE: Chile. S. Francisco del Monte, 1880, *Martio s.n.* (holotype, SGO not seen, photo! [in sched., "typus" by R. Acevedo de V., 1957]).

Solidago valdiviana Phil., Anales. Univ. Chile 87: 431. 1894. TYPE: Chile. Valdivi: San Juan, aestati 1887, *Philippi s.n.* (holotype, SGO not seen, photo! [in sched., "typus," C. Muñez P., 1944]).

Solidago parviflora Phil., Anales Univ. Chile 87: 432. 1894. non *Solidago parviflora* Raf., Ann. Nat. 14. 1820. TYPE: Chile. Pirihuaico, Feb. 1887, *Otto s.n.* (holotype, SGO not seen, photo! [in sched., "typus," R. Acevedo de V., 1957]).

Herbaceous perennials from short to long rhizomes, 7–170 cm; stems erect, glabrate proximally, glabrate to densely canescent distally, hairs 0.05–0.3 mm. Leaves with the proximal ones oblanceolate, twisted, nearly always withering well before flowering; mid-stem leaves usually persisting, in most cases the biggest, sessile, blades linear to oblanceolate, 13–130 × 2–32 cm, with 0 to 12 serrations, abaxial and adaxial faces glabrous or sparsely strigose; distal leaves linear-lanceolate, smaller than proximal, 10–80 × 1–27 mm, with 0 to 10 serrations; inflorescence leaves linear to lanceolate, 4.4–45 × 0.5–18 mm with 0 to 5 serrations. Heads 20 to 200+; in secund lax to dense pyramidal paniculiform arrays, 5–30 × 1–35 cm, branches spreading recurved, second; involucres campanulate, 3.5–5.5 m high; phyllaries in 3 or 4 series, those of outer series ovate, 1.1–2.7 × 0.3–1.6 mm, with inner phyllaries oblanceolate, 0.29–5.1 × 0.3–1 mm, 1 to 3 nerves. Ray florets 7 to 21; laminae yellow, 0.4–3.1 × 0.1–0.9 mm; disk florets 2 to 30; corollas 2.4–4.9 mm, lobes 0.12–3.9 mm. Cypselae body, 0.6–1.5 at anthesis, to 3.3 mm at maturity, sparsely to densely strigose; longest pappus bristles 1.9–5.1 mm. Chromosome count $2n = 18$.

Phenology. *Solidago chilensis* has been observed to flower mainly between December and the end of April and once in late August.

Habitat and distribution. *Solidago chilensis* is known from Argentina (all provinces except for Misiones), Chile, Bolivia, and Uruguay. This species has been found as an introduction in Brazil; Madeira Island, Portugal; Peru; and Puerto Rico. It ranges from latitudes 14°–47°S and longitudes 56°–73°W and elevations from 7 to 2600 m. It is common on roadsides, open grassy plains, and wet soil along streams and springs and is found on sandy soils.

Discussion. The type for *Solidago chilensis* was destroyed at B in 1943, and no Meyen collections remain at B (Voss, pers. comm.). With no original material found, the name is neotypified upon the type of its earliest synonym *S. linearifolia* DC., upon a Née collection.

Solidago chilensis is distinguished by its usually glabrate aspect or with stem hairs mostly 0.05–0.3 mm long; plants from Bolivia tend to be more densely canescent. It is mainly from cold and temperate climates in habitats such as along the roads and in fields and close to water sources (ponds, rivers). In the Patagonian Monte the species forms patches along roads, while in pampas (flatlands) and jungle it reaches further distances from the road within the local flora.

4. Solidago microglossa DC., Prodr. [de Candolle] 5: 332. 1836. *Aster polyglossus* var. *microglossus* (DC.) Kuntze, Revis. Gen. Pl. 3[3]: 131. 1898. TYPE: Brazil. S.d., *Bacle s.n.* (holotype, GDC!, photo sent by G GDC01425_1!, P photo at MO ex Krukoff!).

Solidago microglossa var. *megapotamica* DC., Prodr. [de Candolle] 5: 332. 1836. *Solidago chilensis* Meyen var. *megapotamica* (DC.) Cabrera, Darwiniana 16: 409. 1970. TYPE: Brazil. Prov. Rio Grande: in "hb. Mus. reg. Par. à Mus. imp. Bras. miss. sub n. 846, 854, et 857 [protologue]." *Gaudichaud 854* (holotype, G-DC not seen, photo!, P photo at MO ex Krukoff!).

Solidago marginella DC., Prodr. [de Candolle] 5: 332. 1836. TYPE: Brazil. S. loc., s.d., *Bacle s.n.* (holotype, G-DC not seen, photo!).

Solidago polyglossa DC., Prodr. [de Candolle] 5: 332. 1836. *Aster polyglossa* (DC.) Kuntze, Rev. Gen. 1: 318. 1891. TYPE: Brazil. Rio Grande "v.s. in h. Mus. reg. Par. à Mus. imp. Bras. sub n. 860 missa." s.d., *Gaudichard 860* (holotype, G-DC, photo!, fragm., P photo at MO ex Krukoff!).

Solidago odora Hook. & Arn. var. *scabra* Hook & Arn., Companion Bot. Mag. 2: 45. 1836. TYPE: Uruguay. Monte Video, *Tweedy s.n.* (holotype, K!).

Solidago microglossa var. *macrophylla* Niederl., Bol. Mens. Mus. Prod. Argent. 3, no. 29: 186. 1890, nom. nud.

Solidago bonaerensis Larrañaga, Escritos Damaso Antonio Larranaga 2: 255 [Pub. Inst. Hist. Geog. Uruguay]. 1923, nom. nud.

Plants 36–167 cm tall, stems decumbent from branching rhizome, densely pubescent, canescent. Leaves with the proximal ones oblanceolate, twisted, nearly withering well before flowering; proximal persisting, in most cases the biggest ones of the plant, sessile; proximal blades lanceolate, 22–105 × 5–19 mm, with 0 to 8 serrations, abaxial and adaxial faces pubescent; distal linear to lanceolate, 11–55 × 2–10 mm with 0 to 5 serrations; inflorescence leaves linear to lanceolate, 6–40 × 1–15 mm with 0 or 1 serration. Heads many, in secund pyramidal paniculiform arrays, branches recurved, second. Involucre campanulate, 3.5–6 cm high; phyllaries in 3 or 4 series, those of outer series ovate, 0.17–2.6 × 0.3–0.7 mm, with inner phyllaries oblanceolate, 2.7–4.8 × 0.3–1 mm, 1 to 3 nerves. Ray florets 4 to 28; laminae, yellow, 1–2.9 × 0.1–0.6 mm; disk florets 2 to 14; corollas 2.7–4.5 mm, lobes 0.6–2.3 mm. Cypselae body length at anthesis, 0.4–1.4 mm, strigose; longest pappus bristles 1.8–4.4 mm. Chromosome count $2n = 18$.

Phenology. *Solidago microglossa* has been observed in flower from December until the end of April, with an extension of the flowering period due to favorable weather conditions until mid-spring (October).

Habitat and distribution. *Solidago microglossa* is known from Bolivia, Paraguay, Brazil, and northern Argentina (Misiones, Corrientes, Formosa, Chaco). It has been collected from savannas, open grassy areas, and riversides as well as from secondary vegetation along roadsides and wet grasslands. Collections range from latitudes 7°–39°S, longitudes 34°–67°W, and elevations from 200 to 2740 m.

Discussion. *Solidago microglossa* is characterized by moderately to densely pubescent stems (hairs 0.4–1.2 mm long) and leaves. The species is found mainly in subtropical warm climates, occurring along roads and close to water sources (ponds, rivers). It is inserted as part of the densely local vegetation, such as grasslands and jungle; in Brazil, it is distributed along the coast.

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APPENDIX 1. Chromosome number determinations for *Solidago chilensis* and *S. microglossa* were made from root-tip cells taken from greenhouse-grown plants at the University of Waterloo, Department of Biology, following Owen et al. (2006). Plants were grown from cypselae collected in Argentina and Chile. All vouchers were collected by R. M. Lopez Laphitz and L. A. Becker (*LL & B*) and have been deposited in WAT with duplicates in LP.

Solidago chilensis Meyen., $2n = 18$.

ARGENTINA. **Buenos Aires:** Saldungaray, a. Al lado de la RP 72, *LL & B 4*. **Catamarca:** RN 38 hacia San Fernando del Valle de Catamarca, *LL & B 27*. **Chubut:** Gaiman, camino La Angostura hacia Dolavon, *LL & B 7*; Casi Epuyen, RN 40 desde Esquel, *LL & B 12*. **Cordoba:** Vickuna Mackenna, RN 35, *LL & B 20*. **Entre Rios:** RN 127 entre San Jaime de la Frontera y los Conquistadores, *LL & B 50*. **La Pampa:** RN 35, empalme con RP 10, *LL & B 19*. **La Rioja:** RN 141 y 79, *LL & B 26*. **Mendoza:** Monte Coman, RP 171, *LL & B 23*. **Neuquen:** RN 40, Km. 2069 casi limite con Rio Negro–Neuquen, *LL & B 14*; Junin de los Andes, *LL & B 16*; RN 40, camino de Junin de los Andes a Zapala, *LL & B 17*. **Rio Negro:** limite Rio Negro y Neuquen, RN 40 pasando Dique Alicurá 20 km hacia Neuquen, *LL & B 15*. **Salta:** RN 16 entre El Tunal y El Galpon, *LL & B 39*. **Santa Cruz:** Los Antiguos, *LL & B 9*. **Santa Fe:** Venado Tuerto, RN 8, *LL & B 1*; RP 95 pasando Pozo Borrado, *LL & B 34*; RN 127, *LL & B 51*. **Santiago del Estero:** RN 34 a 15 km sur del empalme con RP 92, *LL & B 31*; RN 64, a. A 3 km de Santiago del Estero, *LL & B 30*. CHILE. **Region XI:** ruta 265 (Camino Austral), a. Al lado de El Fachinal, *LL & B 10*.

Solidago microglossa DC., $2n = 18$.

ARGENTINA. **Chaco:** RN 16, a. A 10 km O de Roque Saenz Peña, *LL & B 36*; RN 16, saliendo del Puente General Belgrano, *LL & B 42*. **Corrientes:** Santo Tomé, *LL & B 47*; RN 123 entre RP 119 y RP 29, *LL & B 48*. **Formosa:** RN 11 llegando a Formosa Capital, *LL & B 43*; RN 81 pasando Estanislao del Campo, *LL & B 41*.